ETHYLENE AND FLOWER INDUCTION

IN GUAVA PSIDIUM GUAJAVA L.

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ABSTRACT

Ethephon-urea sprays, branch bending, and silver nitrate were used to test the roles of ethylene in flower induction in young, clonal guava, Psidium guajava L. Branch bending with or without silver nitrate pretreatment, a low concentration ethephon-urea spray applied four times at five day intervals, and a high concentration ethephon-urea spray applied once with silver nitrate pretreatment increased flowering compared to controls. Ethylene content in stem tissue two days after treatment was positively correlated with the number of laterals produced and negatively correlated with extension growth 18 days after treatment. Ethylene content and reduction in growth were not correlated with flowering. A reduction in apical dominance was highly correlated with flowering.

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INTRODUCTION

The guava, Psidium guajava L., originated in the American tropics and from there was distributed throughout the tropics and subtropics (77, 132, 145).

The guava tree produces a perishable fruit which is used in tropical and subtropical countries to make a wide variety of sweetened products. In some countries, sweet guavas are grown for the fresh market (55, 69, 77, 132, 145).

In Hawaii, acid type guavas are grown commercially for processing. In 1979, there were 890 acres planted with 565 acres in production. The average yield was 7965 pounds per acre (13).

Collecting guavas from the wild cannot be relied upon for a consistent supply of good quality fruit. Presently, optimum yields in commercial orchards are not being achieved and growers cannot meet the demands of processors. Some of the production problems include: 1) planting of seedling trees which are genetically variable and which take longer to come into bearing because of juvenility, 2) erratic bearing habit of guavas so that growers with large acreages cannot rely on natural environmental factors to stimulate uniform flowering, and 3) lack of well defined modern cultural practices.

Studies of changing and controlling the seasonal production of guavas by cultural methods such as branch bending, defoliation, pruning, and fertilization with irrigation are promising. Results show that guava trees can be manipulated by cultural practices to produce fruit at different times of the year (14, 35, 55, 69, 77). In apples, these cultural practices induce the production of stress ethylene which results

in leaf abscission, reduction in growth, reduction in apical dominance, and in flower initiation (86, 97, 128, 129, 164).

It is the purpose of this study to test the roles of ethylene, a gaseous plant growth regulator, on flower induction in young, clonal guava trees. The results of this study may provide a theoretical basis on which to manipulate present cultural practices to suit the needs of commercial growers.

Although direct evidence would be difficult to produce, indirect evidence of the roles of ethylene in guava flower induction will be sought by the following methods:

1) measurement of relative ethylene content in stem tissue, lateral production, and extension growth among ethephon-urea treated trees and trees stressed by branch bending to determine if these parameters are associated with flower induction;
2) use of an inhibitor of ethylene action, silver nitrate, to determine if ethylene induced responses and flowering can be inhibited;
3) use of a low concentration ethephon-urea spray to determine if flowering can be induced without excessive leaf abscission; and
4) measurement of fruit set to determine if any of the treatments have practical application.

LITERATURE REVIEW

GUAVA

Systematics

The guava belongs to the Myrtaceae or Myrtle family. This large botanical family is divided into two subfamilies, the primarily fleshy fruited Myrtoideae with about 32 genera of worldwide tropical and subtropical distribution, and the primarily capsular fruited Leptospermoideae with about 40 genera which are mainly restricted to the Australasian region. The genus Psidium, in which there are about 150 species, belongs to the Myrtoideae. Presently, the guava, Psidium guajava Linn., is the most economically important species. The generic name is derived from the Greek word pziso which means to feed on pap and the specific epithet guajava is derived from the Spanish word guayaba which means guava tree (15, 32, 77).

Structure in Relation to Flowering

In its natural environment, the guava grows into a large shrub which branches freely from the base and tends to maintain apical dominance which is shown by the growth of tall, vertical shoots with few well developed side branches, but when cultured, well developed trees up to 10 m have been obtained.

Guava leaves are usually decussate with an axillary bud in each leaf axil. Axillary buds may differentiate into vegetative shoots or flowers. Vegetative shoots produced by axillary buds are referred to as laterals. The axillary buds on these laterals may in turn differentiate into flowers or remain vegetative. In guava, the

production of flowering laterals is the main factor to increase yields. Usually axillary buds differentiate directly into flowers on terminal shoot growth. Occasionally, determinate inflorescences are produced. Whether they occur in the axils of laterals or terminals, guava flowers are produced only on new growth and since new growth occurs throughout the year, flowers and fruits of varying maturity on a given tree can usually be found.

Guava flowers are hermaphroditic and are about 2.5 cm in diameter. These occur singly or in two to three flowered cymes (16, 32, 117).

The duration of the flowering period in guava depends on the cultivar and on the environmental conditions. Anthesis and dehiscence occur in the early morning and take about two hours to complete. Self pollination is relatively high, but insects attracted to the nectar and pollen do facilitate some cross pollination (16, 32, 56, 116, 137, 143, 146).

The fruit produced after pollination and fertilization is a berry which varies in shape, size, color, texture, flavor, and acidity (32, 117, 132). Guava fruits take five to eight months to mature depending upon the environmental conditions during fruit growth and development (12, 69).

ETHYLENE

Introduction

Ethylene (C_2H_4) is recognized as a gaseous growth hormone because it possesses properties of a typical plant growth hormone and for its participation in a wide variety of plant processes. Many of these ethylene effects are of horticultural interest (5, 37, 87, 119, 123, 168).

Ethylene is the simplest unsaturated alkene. It is a flammable, colorless gas with a boiling point of -103°C; a density of 0.978; and a molecular weight of 28.05 (159).

Since ethylene is a gas, it also possesses some properties not associated with that of a typical plant hormone, for example, no transport system is required; ethylene moves from the site of production to the site of action along a concentration gradient. In addition, ethylene levels are reduced by diffusion to the surrounding atmosphere and no mechanism to metabolize it is required (5, 37, 123).

Many of the responses to ethylene in different plant materials have similar dose response curves suggesting that a single mode of action of the gas is involved (5, 38, 40). Although low concentrations of the gas can cause a near maximal response, higher concentrations usually intensify it without producing secondary phytotoxic effects (2, 102). Under normal conditions, any living plant cell can produce ethylene, but the amount produced is usually very low (5, 168).

Detection and Identification of Ethylene in Vegetative Plant Tissues

Ethylene can be detected and quantified in gas samples from plant tissues by gas chromatography. Prior to the widespread use of gas chromatography, detection of the gas was often by the triple response bioassay in etiolated peas (37, 159). The gas chromatograph has the advantages of speed, sensitivity, and quantitative response (36, 37, 123, 158, 159).

In ethylene analysis, gas solid chromatographs with activated alumina columns and flame ionization detectors are usually used. Ethylene is identified by comparing retention times of sample chromatographic peaks with ethylene standards under constant conditions and by quantitative absorption with mercuric perchlorate (2, 28, 37, 83, 86, 101, 104, 128, 129, 159). Peak areas can be used to quantify the amount of ethylene in gas samples (95, 104), but peak heights involve less errors under constant conditions and are normally used (159). Calibration graphs are suggested, but when sensitive flame ionization detectors are used, sample injections are difficult to reproduce (36, 95).

Ethylene samples from plant tissues are collected in various ways, some of which involve detachment of plant parts and subjecting them to a vacuum (25, 28, 83, 86, 128, 129, 159), while others involve diffusion of ethylene from intact or detached plant parts (156, 157). Evacuation of tissues does not alter its metabolism, but removes bound ethylene, ethylene in solution, and ethylene from the intercellular spaces (25, 37). When reduced pressures of less than 100 mm Hg are used, wound ethylene is produced (25, 134).

When plant parts are detached, wound ethylene usually results, therefore, cut surfaces should be minimized (101). Wound ethylene production also increases if the period between detaching and extraction is prolonged (28). In some plant tissue, the length of time before a rise in wound ethylene production occurs is known (78). Other factors which may contribute to elevated ethylene levels include atmospheric ethylene and ethylene from parts of the apparatus. Blanks without tissue samples are used to detect this (83, 159). Samples should be collected at the same time because in some plants, ethylene levels fluctuate at different times of the day (28, 83).

Biosynthesis of Ethylene

Radioactive tracer studies with ^{14}C-labeled methionine in non-enzymatic model systems show that carbons three and four of methionine produce ethylene (88, 90, 92). Methionine is also the precursor in the biosynthesis of ethylene (17, 18, 19, 89, 90, 92). Recently, evidence for the intermediary steps involved in ethylene biosynthesis from methionine have been described. The rate limiting step of these reactions is the conversion of S-Adenosylmethionine (SAM) to 1-Aminocyclopropane-1-carboxylic Acid (ACC) by ACC synthase (10, 11, 29, 108, 168, 170). In some plant tissues, the addition of ACC stimulates ethylene production (48, 84).

There are several factors which inhibit ethylene biosynthesis and these include inhibitors of ACC synthase, dinitrophenol, low oxygen concentration, high carbon dioxide concentration, temperatures greater than 30°C, and cobalt (II) (5, 11, 29, 37, 44, 46, 84, 87, 88, 89, 109, 120, 124, 168, 170, 172, 173).

Indoleacetic acid (IAA) stimulates ethylene production in plants (42, 68, 80, 119). IAA is necessary for the formation of ACC synthase and auxin induced ethylene production is the result of an increase in ACC synthase. As in natural ethylene production, methionine is the precursor (136, 168, 171, 173).

Stress Ethylene

In response to changes in environmental conditions, plants produce higher levels of ethylene than normal. The production of this stress or wound ethylene depends on the plant tissue, nature, and intensity of the stress. Only living, intact cells adjacent to the injured or dead cells produce stress ethylene; the more severe the damage is, the greater the production of stress ethylene by the living cells (1, 34, 72, 87, 133, 147, 169).

The biosynthesis of stress ethylene is similar to natural and IAA induced ethylene production. Although the mechanisms differ, methionine is the precursor and the stress induces the synthesis of ACC synthase which converts SAM to ACC (1, 87, 168, 169, 174).

Chemical, biological, and physical stresses induce plants to produce stress ethylene. Examples of these are chemical defoliants, insects, and bending (2, 169).

In debladed tomato stem tissue, the rate of ethylene production in horizontal stems is three times greater than in vertical stems (63). A higher rate of ethylene production is due to a greater auxin content and therefore the shoot tips of horizontal stems produce more ethylene because they are the sites of auxin synthesis (5). Stress ethylene in

bent apple shoots is greater near the shoot tips and decreases linearly toward the basal ends of the branches. It is also significantly greater on the underside of horizontal shoots (128, 157). Stress ethylene in bent branches usually results in a decrease in elongation growth. The production of stress ethylene in bent branches is the result of stress and not of wounding (86, 129).

Ethephon

Ethephon is the approved common name of (2-Chloroethyl)Phosphonic Acid. Ethephon is stable in aqueous solutions below pH 4.0, but at higher pHs it degrades to release ethylene. In buffered solutions, ethephon has a half life of 5.6 days at pH 6.1 and 20°C, but at 30°C, the half life is 26.5 hours. Ethephon therefore provides a practical way to stimulate ethylene induced responses in plants and as a result, it is widely used in agriculture and in physiology (30, 64, 66, 118, 161, 167).

Ethephon is taken up by plants and subsequently degrades in cytoplasmic pH to release ethylene. The uptake and breakdown of ethephon in plant tissues increases as the temperature increases (58, 94, 118, 161, 167). Radioactive tracer studies show that ethephon is generally translocated in a source to sink manner and that young tissues with less cuticle absorb and translocate more of the chemical. Ethephon applied to fruit is not readily absorbed. In ethephon treated sour cherry leaves, most of the ethylene evolved results from the degradation of ethephon rather than from the stimulation of ethylene biosynthesis. Complete spray coverage is necessary because ethephon is translocated slowly. The effectiveness of low concentrations of ethephon can be

increased with the addition of urea which increases the absorption of ethephon and by calcium carbonate which increases the pH of the solution (61, 65, 100, 118, 162, 165, 166).

Inhibition of Ethylene Action by Silver Nitrate

Silver (I) is an effective inhibitor of ethylene responses, for example, it inhibits ethylene induced triple response of etiolated peas and prevents ethylene induced flower, fruit, and leaf abscission in several plants (20, 21, 23). Other metal ions are not as effective and the nitrate ion is not responsible for the effect (21, 23, 135, 155). At physiologically active concentrations, silver nitrate ($AgNO_3$) is not phytotoxic, but ethylene production and phytotoxic symptoms occur at higher concentrations (21, 23, 135). Small increases in exogenous ethylene do not overcome the effects of Ag(I), but large increases in ethylene do (20, 24). It is suggested that Ag(I) reduces the sensitivity of the tissue to ethylene by interfering directly with ethylene action at the receptor site which may be a metallic receptor site such as copper (I) (20, 21).

Roles of Ethylene in Leaf Abscission

Abscission is the process of shedding plant parts such as leaves, flowers, and fruits and involves abscission zone differentiation, separation, and protective layer formation (85).

Auxins inhibit or promote leaf abscission depending on the maturity. Ethylene either has no effect or promotes abscission depending upon the age of leaf (131).

In young leaves, the endogenous auxin content is higher than in older leaves and is described as stage I. This high auxin concentration prevents aging, senescence, and abscission zone differentiation. During this time, endogenous ethylene has no effect in stimulating abscission zone differentiation (6, 26, 27, 38, 74, 85).

As the leaf ages, the auxin concentration in the blade and in the petiole declines due to a decrease in basipetal auxin transport capacity, a decrease in auxin synthesis, or an increase in auxin destruction. This stage of leaf development is described as stage II and is associated with reduced auxin content and increased sensitivity to ethylene induced leaf abscission (4, 8, 22, 26, 38, 74, 85). Stage II leaves can be induced by exogenous ethylene or by environmental stress induced ethylene which causes the leaf to age and senesce (74).

Exogenous ethylene promotes abscission by aging the tissue which subsequently reduces the effective concentration of auxin into the petiole and is also involved in the synthesis and secretion of cellulase, a cell wall degrading enzyme. The abscission process can be stopped if ethylene is removed before actual separation occurs (5, 7, 8, 9, 22, 26, 27, 38, 74, 85, 119).

If stage I plant material is treated with auxin prior to ethylene, abscission does not occur, but application of auxin to stage II plant material cannot reverse the aging process and the ethylene stimulated by auxin causes abscission of the plant organ. This shows that during stage I, the effect of auxins is greater than the effect of auxin induced ethylene production and that sensitivity to ethylene occurs only when the tissue has aged (6, 8, 74).

Promoters of leaf abscission have been known to either stimulate ethylene biosynthesis or to degrade into ethylene. Substances which have little effect on abscission, usually do not result in elevated levels of ethylene in plant tissues (4, 60, 62, 67, 73, 123, 131).

In leaf abscission, the amount of ethylene required to produce a threshold, half maximal, and a complete response is similar for different plants (38).

Roles of Ethylene in Vegetative Growth

Plants exposed to ethylene respond in a variety of ways, for example, etiolated pea plants show a decrease in elongation growth, stem swelling, and loss of geotropic response. These effects are known collectively as the triple response (39, 102).

Ethylene gas and ethephon stimulate isodiametric growth by altering the deposition of newly formed cellulose microfibrils during cell wall formation. The microfibrils in ethylene treated plants are deposited in a longitudinal rather than in a transverse direction so that radial expansion is promoted and longitudinal expansion is inhibited. Ethylene may inhibit elongation growth by blocking cell division in the meristem and by decreasing DNA synthesis (39, 40, 102, 119, 160). Treatment of apple stem tissue with ethephon results in higher ethylene contents and is associated with a decrease in extension growth and an increase in diameter growth (129, 157).

Application of ethylene and ethephon to plants inhibits the growth of lateral buds, but later increases the number of lateral shoots when the treatments are terminated (40, 45, 67). The presence of ethylene

can inhibit mitotic activity and outgrowth of lateral buds even when the stem apex is removed. It is suggested that in intact plants, ethylene stimulates lateral bud growth by reducing apical dominance even though the gas inhibits lateral bud growth when it is present. The reduction in apical dominance may be due to the effect of ethylene on auxin metabolism and transport (3, 39, 40, 43, 91, 105, 151).

FLOWER INDUCTION IN SOME FRUIT CROPS

Flower initiation is the first step in the transition from vegetative to reproductive growth and at present very little is known about the mechanisms involved for different plants (175, 176).

In some fruit trees, several factors are associated with flower induction, for example, flowering usually occurs only after a period of juvenility and at which time the plant has accumulated sufficient carbohydrate reserves. Secondly, the environmental conditions must be conducive to reproductive rather than to vegetative growth and this may involve a change in the balance of plant growth hormones. Finally, the accumulation of essential plant metabolites at the meristem is necessary for the initiation of cell division and differentiation of flower primordia (81, 97, 164).

Although this is highly simplified and many other factors are involved, there is evidence which supports these basic associations, for example, even though a tree has reached maturity, the presence of environmental conditions conducive to vegetative growth oftens results in little or no flower initiation (49, 113). Some fruit trees usually bloom after a period of physiological stress followed by conditions which stimulate growth, for example, in India there are distinct

flowering seasons for guava which results from dry and wet seasons (16, 35, 55, 56, 69, 77, 116, 137, 146). In Hawaii, however, distinct dry and wet seasons usually do not occur and guavas are produced throughout the year (140). Another example is the litchi in which a period of low night temperatures and high moisture stress are required for flower initiation and a period of adequate moisture is needed for growth and development of flowers and fruits. If rain occurs during the flower initiation period, vegetative rather than reproductive growth results (113, 114, 115).

In some fruit trees which produce flowers on lateral growth, the terminal bud inhibits flower initiation. The terminal buds of vertical apple shoots have higher levels of auxin and gibberellic acid (GA) like substances compared to horizontal shoots and vertical shoots grow more vigorously (81, 96). The GA produced in the young leaves moves to the apex and stimulates the production or downward movement of auxin which promotes the transport of carbohydrates and organic nitrogen to the apex which maintains apical dominance (96). It is felt that a temporary reduction in terminal shoot growth during the critical flower initiation period is necessary so that metabolites can move to the lateral buds to stimulate cell division and flower initiation. There are several cultural practices which temporarily reduce shoot growth and release the correlative inhibition of the shoot tip during the critical flower initiation period (49, 97, 98, 126, 127, 144, 154).

In guava, the production of flowering laterals is the main factor for increasing yields and therefore cultural practices are aimed towards stressing trees followed by stimulation of growth in such a way that

growth of laterals rather than terminal shoots is favored. In India, pruning and branch bending are used. In addition, guava trees can be stressed by withholding water until the leaves abscise followed by irrigation and fertilization (14, 55, 69, 77). Pruning in guava reduces apical dominance, but does not eliminate it. If a vertical branch is cut between side branches, vigorous new growth usually results near the cut, but if the cut is made to a side branch, apical dominance will be reduced, but maintained to a certain extent by the side branch and laterals will be stimulated to grow along the length of the remaining vertical branch (140, 141).

Reduction in shoot growth occurs when small apple trees or branches of apple trees are placed in a horizontal position (76, 103, 107, 148, 149, 150), but flowering is not always promoted. It is suggested that the initiation of flower buds in apples is not always associated with a reduction in shoot growth and that these are two partially independent phenomena (149). Bending is effective if trees are vigorous, but not if trees are low to moderate in vigor, in which case a reduction in shoot growth to stimulate flower initiation in the lateral buds is not necessary (103, 164). The presence of fruits on bent branches also inhibits flower initiation by creating stronger sinks for essential plant metabolites which may be due to the endogenous GA of seeds (97, 148). In Java, two crops of apples per year are produced by removing the terminal leaves near the developed flower buds when they are at right angles to the spur on the stem axis. The trees are trained to a vase system and the uppermost branches are tied down with strips of plastic tape which stimulates the development of upright spurs evenly

along the branch. The terminal ends of the bent branches are headed back which produces dwarf trees (79).

Growth regulators are used to alter the balance of plant hormones so that reproductive growth is favored, although effective in some cases, they usually have no effect, at nonphytotoxic concentrations, if the trees are extremely vigorous or juvenile (164).

Smoke or ethylene gas can stimulate flowering in pineapple and in mango (59, 70, 130). Auxins are also effective in stimulating flowering in pineapple and litchi by inducing ethylene production (41, 57, 59, 113, 138, 152, 153).

Ethephon and ethephon-urea sprays stimulate flower formation in pineapple, mango, and guava. In guava, high concentrations of urea or ethephon-urea sprays are used to stimulate the production of flowering laterals by defoliation. Low concentration ethephon-urea sprays stimulate the production of axillary inflorescences in "off" year biennial bearing mango without leaf abscission. Higher concentrations of ethephon can induce flowering in juvenile mango trees (51, 52, 53, 54, 61, 121, 125, 139, 140, 141, 142). In addition to ethephon, growth retardants such as CCC, and chemicals such as potassium nitrate are effective in inducing flowering in mango (31, 98, 99, 125).

In apple, ethephon-SADH sprays are effective in controlling growth and in stimulating flower initiation in vigorous trees and in nonbearing seedling trees. In spur type trees, these sprays result in an increase in lateral branching and reproductive spur formation. Apical dominance is reduced by the combined effects of ethephon on auxin metabolism and transport and of SADH on GA metabolism. These treatments result in a

redirection of metabolites to the spur buds rather than to the terminal buds and it is suggested that a reduction in shoot growth is not the direct cause of flower initiation (47, 71, 82, 93, 97, 150, 154, 163, 164).

Under natural conditions, some fruit trees have evolved to initiate flowers under periods of physiological stress and to begin growth and development of the flowers when more favorable conditions are present (77, 114). Cultural practices can also be used to stress trees. The production of stress ethylene may indirectly influence flower initiation by reducing growth and by releasing the lateral buds from the correlative inhibition of the terminal bud, but evidence for ethylene as the flower inducing hormone has not yet been shown.

MATERIALS AND METHODS

Field experiments were conducted at the Waimanalo Research Station located on the windward side of the island of Oahu about 33 km from the University of Hawaii, Manoa. The station is two km from the Pacific Ocean at an elevation of 17 m.

During 1980, the mean monthly rainfall was 12 cm with the highest rainfall occurring during January, May, and December. The mean monthly temperature was 24°C and the mean monthly solar radiation was 327 g cal per cm^2 per day with the highest solar radiation occurring from April to September. The soil type of the area is a Waialua gravelly clay soil (Vertic Haplustolls).

The experiments were on clonal 'Beaumont' (12, 33, 75, 112) and 'Ka hua kula' (12, 110, 111) guava trees. There were 160 trees of each cultivar which were spaced at 2.4 m in rows and about 6.1 m between rows. At the time of the experiments, the trees were about two years old and most had already produced flowers and fruits.

Supplemental irrigation was from a drip system. Weed control in the field consisted of periodic sprays of herbicide within the rows and mowing between the rows. Insecticides were used to reduce the population of spiralling whiteflies (Aleurodicus dispersus, Russell).

The trees were not pruned except to maintain a single trunk and to remove lower branches. Fertilizer applications were also kept to a minimum. Excessive pruning and fertilization were avoided to prevent their effect on stimulating the growth of laterals during the experimental period.

Chemical solutions were based on the concentration of active ingredient on a weight to volume basis and were prepared just prior to application. Ethephon from Ethrel was calculated on the basis of four pounds ethephon per gallon. Silver nitrate sprays were prepared with analytical grade $AgNO_3$. Ethephon-urea sprays were applied with a one gallon stainless steel sprayer. Silver nitrate sprays were made with deionized water to prevent reaction to AgCl and were applied with an all plastic sprayer to prevent reaction with metal parts. Tween 20 at 0.1% was added to all $AgNO_3$ sprays. All sprays were applied to runoff and the amount of spray applied per tree was estimated. On windy days, spray drift was minimized by holding the sprayer nozzle close to the leaves and by reducing the pressure which increased droplet size.

A randomized complete block design was used in all experiments. To minimize homogeneity of errors, treatments and replications were randomized using a table of random numbers.

Countings and measurements were done at least twice and mean values were used.

EFFECT OF ETHEPHON-UREA SPRAYS ON LEAF ABSCISSION

A preliminary experiment was conducted to determine a concentration of ethephon-urea spray which would not cause excessive leaf abscission. The selected treatment was used in another experiment to test the effect of a low concentration ethephon-urea spray applied four times at five day intervals on flower induction without excessive leaf abscission.

In this experiment, 'Beaumont' trees were used. Prior to treatment application, five branches were tagged on each tree and the leaves per

branch were counted. There were two replications and five treatments which were: 1) control with no ethephon or urea, 2) 200 ppm ethephon + 1% urea, 3) 400 ppm ethephon + 1% urea, 4) 600 ppm ethephon + 1% urea, and 5) 1000 ppm ethephon + 6% urea.

On June 18, 1980, the trees were sprayed at 8:30 A. M. The temperature was 26°C. No surfactant was used in these sprays and the amount of spray per tree was about one liter. One week after the treatments were applied, the leaves remaining per branch were counted and the percentage leaf abscission calculated.

EFFECT OF SILVER NITRATE ON ETHEPHON-UREA INDUCED LEAF ABSCISSION

A second preliminary experiment was done to determine the effect of silver nitrate ($AgNO_3$) in inhibiting leaf abscission induced by 1000 ppm ethephon + 6% urea. The selected treatment was used in another experiment to determine its effect in inhibiting flower induction by the ethephon-urea spray and by branch bending. The application of $AgNO_3$ prior to the ethephon-urea spray and branch bending will be referred to as $AgNO_3$ pretreatment.

In this experiment, 'Ka hua kula' trees which were smaller than the 'Beaumont' trees were used. There were two replications and eight treatments which were: 1) complete control with no $AgNO_3$ pretreatment or ethephon-urea spray, 2) partial control with 100 ppm $AgNO_3$ and no ethephon-urea spray, 3) partial control with 200 ppm $AgNO_3$ and no ethephon-urea spray, 4) partial control with 400 ppm $AgNO_3$ and no ethephon-urea spray, 5) 0 ppm $AgNO_3$ (distilled water) pretreatment followed by 1000 ppm ethephon + 6% urea, 6) 100 ppm $AgNO_3$ pretreatment

followed by 1000 ppm ethephon + 6% urea, 7) 200 ppm $AgNO_3$ pretreatment followed by 1000 ppm ethephon + 6% urea, and 8) 400 ppm $AgNO_3$ pretreatment followed by 1000 ppm ethephon + 6% urea. Silver nitrate sprays were applied about 36 hours before the ethephon-urea spray.

The $AgNO_3$ sprays were applied on July 15, 1980, at 5:30 P. M. The temperature was 27°C and about 500 ml were applied per tree. On July 17, 1980, at 7:00 A. M., the 1000 ppm ethephon + 6% urea treatment was applied to the trees pretreated with $AgNO_3$. The temperature was 26°C and a passing shower occurred at 8:30 A. M. which produced 0.38 cm of rain. Percentage abscission was calculated as in the previous experiment.

EFFECTS OF ETHEPHON-UREA SPRAYS, BRANCH BENDING, AND SILVER NITRATE ON RELATIVE ETHYLENE CONTENT, LATERAL PRODUCTION, FLOWER FORMATION, FRUIT SET, AND EXTENSION GROWTH

After the preliminary experiments, the selected treatments were used to determine the effects of a high concentration ethephon-urea spray (1000 ppm ethephon + 6% urea), a low concentration ethephon-urea spray (200 ppm ethephon + 1% urea), and branch bending on various parameters such as relative ethylene content of stem tissue, lateral production, flower formation, fruit set, and extension growth. Silver nitrate was also used to determine the role of ethylene in these parameters.

In this experiment 'Beaumont' trees were used. Before the treatments were applied, ten branches were tagged on each tree. Five branches were used for ethylene samples, a branch for each of the five sampling dates, and four branches were used for flowering data. The

terminal shoot was used to measure extension growth. The existing laterals and shoot tips were tagged so that these could be distinguished from new laterals and shoot tips.

There were eight replications and six treatments which were: 1) control with no treatment, 2) 1000 ppm ethephon + 6% urea, 3) 100 ppm $AgNO_3$ pretreatment followed by 1000 ppm ethephon + 6% urea about 24 hours later, 4) 200 ppm ethephon + 1% urea applied four times at five day intervals, 5) branch bending, and 6) 100 ppm $AgNO_3$ pretreatment followed by branch bending about 24 hours later.

The 100 ppm $AgNO_3$ spray was applied on August 21, 1980, at 5:30 P. M. The temperature was 27°C and about one liter of spray was used per tree. Sprays were applied in the afternoons because generally, there was less wind and not as many brief, passing showers as in the mornings.

On August 22, 1980, the branches were bent and the ethephon-urea sprays were applied. Branches were bent by tying with 8 mil vinyl grafting tape about 30 cm from the shoot tip and tied to pegs set in the ground. The force used to bend the branches was not determined and the angle of bending depended on the initial angle of the branch to the main axis.

At 5:30 P. M. of the same day, the first 200 ppm ethephon + 1% urea spray and the single 1000 ppm ethephon + 6% urea spray were applied. The temperature was 28°C and about one liter of spray was used per tree. The other 200 ppm ethephon + 1% urea sprays were applied on August 27, September 1, and September 6, 1980. On all three spray dates the

temperature was 28°C at about 5:00 P. M. and about 900 ml of spray were applied per tree.

Branches were released from the bent position on September 9, 1980, and at this time, preexisting flowers and fruits were removed from all trees except that flowers on the control trees were left on. Prior to this, flowers and fruits initially present on the trees were left on to observe the effects of the treatments on abscission.

Relative Ethylene Content

Ethylene content of stem tissue was estimated by using a modification of the method of Klein and Faust (83). Tissue samples were collected from each tree on five sampling dates which were 0 (prior to treatment), 2, 4, 8, and 16 days after treatment. On each sampling date, at about 9:00 A. M., tagged branches were removed at the 5th internode from the shoot tip, the time was recorded, and the samples were brought to a location out of direct sunlight for preparation. A five cm stem piece including the node of the third mature leaf from the tip was used to standardize the procedure.

The prepared tissue sample was then placed in a 12.5 cc vacu-tainer and sealed. A vacuum was created by inserting the needle of a 20 cc syringe, withdrawing the plunger to the 18.7 cc mark, and propping it with a piece of wooden dowel which was cut so that the plunger remained at that level. The pressure in the vacu-tainer measured with a vacuum gauge was 323 mm Hg. Blanks without tissue samples were also prepared.

Analysis for ethylene consisted of removing the vacuum from the vacu-tainer and taking a one ml sample of gas with a three cc syringe.

The gas sample was immediately injected into a Varian 1400 series gas chromatograph equipped with a flame ionization detector and alumina column. The column temperature was 90°C and the detector and injector temperatures were 110°C. Nitrogen was used as the carrier gas and the flow rate was 25 ml per minute. The recorder speed was one cm per minute and under these conditions, the retention time of ethylene was one minute (Figure 1).

Ethylene was identified by retention time and peak areas were used to quantify the amount of ethylene in the samples. Ethylene content was expressed as nl/g/hr.

Lateral Production

Lateral production parameters were used to determine the effect of the treatments on apical dominance. Days to lateral emergence were determined by counting the axillary buds per branch which showed signs of growth at three to four day intervals from September 1, to September 24, 1980. Axillary buds per branch were counted prior to the application of treatments and laterals counted about one to two weeks before anthesis and the percentage of axillary buds forming laterals and the number of laterals per 20 axillary buds were determined.

Flower Formation

Days to 50% anthesis were determined by the length of time it took for about half of the flower buds to open on each branch. Open flowers per branch were counted at three to four day intervals starting from October 18, to November 22, 1980.

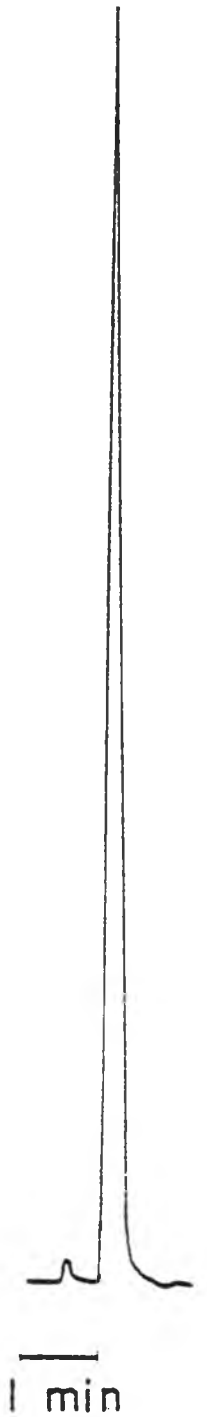

Figure 1. Gas chromatogram of ethylene standard. One cc of 1006 ppm ethylene was used. Actual size of chromatogram. Attenuation = X32.

Flowers per lateral per branch were counted when they were plainly visible about one to two weeks before anthesis and the percentage of laterals with flowers and the number of flowers per 20 axillary buds were determined.

Flowers were also counted per shoot tip per branch and the percentage of shoot tips with flowers was determined. Shoot tips also included existing laterals.

Fruit Set

Fruits per lateral per branch were counted about 50 days after anthesis so that only the fruits left after the main fruit drop period would be included and percentage fruit set in laterals and the number of fruits per 20 axillary buds were determined. Percentage fruit set in shoot tips was also determined.

Extension Growth

Extension growth was measured on terminal shoots 18, 79, and 140 days after treatment.

Analysis of Data

Ranges of the treatments were plotted against their means and if a relationship was observed, $\log_{10}$ transformations were used to normalize the data. Arcsin transformation was used with percentage data. In data collected from branches, experimental units were trees and branches were samples. All data were analyzed by analysis of variance and the treatment means were separated using Duncan's multiple range test. When transformed data were used, the transformed data means were used, but

means presented in the tables were treatment means calculated from the untransformed data.

Since an inadequate number of standards was used to allow comparisons of ethylene contents among days, ethylene contents were analyzed within days only.

In the percentage fruit set in shoot tips analysis, branch bending with and without $AgNO_3$ pretreatment were omitted because of poor flowering.

Simple linear correlations were on these parameters:

1) ethylene content two days after treatment and number of flowers per 20 axillary buds,
2) extension growth 18 days after treatment and number of flowers per 20 axillary buds,
3) number of laterals per 20 axillary buds and number of flowers per 20 axillary buds,
4) ethylene content two days after treatment and extension growth 18 days after treatment,
5) ethylene content two days after treatment and number of laterals per 20 axillary buds, and
6) number of flowers per 20 axillary buds and percentage fruit set in laterals.

RESULTS

EFFECT OF ETHEPHON-UREA SPRAYS ON LEAF ABSCISSION

Ethephon at 1000 ppm + 6% urea results in severe marginal scorching and necrotic spotting of the leaves. One week after the treatments were applied, there was a significant difference in the percentage of leaves which abscised from the 1000 ppm ethephon + 6% urea spray and the other treatments. There was no significant difference among the control and 200, 400, or 600 ppm ethephon with 1% urea (Table 1). Most of the flowers and fruits initially present on trees sprayed with 1000 ppm ethephon + 6% urea or with 600 ppm ethephon + 1% urea abscised within seven days, but flowers and fruits on control trees did not abscise. The lowest ethephon concentration + 1% urea did not result in damage to the leaves or in excessive leaf, flower, and fruit abscission and was selected for use in another experiment to determine its effect on flower induction when sprayed four times at five day intervals.

EFFECT OF SILVER NITRATE ON ETHEPHON-UREA INDUCED LEAF ABSCISSION

One week after the treatments were applied, there was a significant difference in percentage leaf abscission between all trees treated with ethephon-urea and trees which did not receive ethephon-urea. There was no significant difference between complete and partial controls. In trees sprayed with 1000 ppm ethephon + 6% urea, there was no significant difference among trees pretreated with 0, 200, or 400 ppm $AgNO_3$, but there was a significant difference between trees pretreated with 100 ppm $AgNO_3$ and trees pretreated with 0 or 200 ppm $AgNO_3$ (Table 2). The 100 ppm $AgNO_3$ pretreatment was selected to test its effect in flower

Table 1. Effect of ethephon-urea sprays on leaf abscission in 'Beaumont' guava trees seven days after treatment.

Treatment	Percentage Abscission[z]
Control	0.4[b]
200 ppm ethephon + 1% urea	12.7[b]
400 ppm ethephon + 1% urea	16.2[b]
600 ppm ethephon + 1% urea	14.9[b]
1000 ppm ethephon + 6% urea	71.8[a]

[z] Means followed by the same letter are not significant, 5%.

Table 2. Effect of silver nitrate ($AgNO_3$) on ethephon-urea induced leaf abscission in 'Ka hua kula' guava trees seven days after treatment. Silver nitrate sprays were applied about 36 hours before the ethephon-urea spray.

Treatment	Percentage Abscission[z]
Control	1.4[c]
100 ppm $AgNO_3$	0.9[c]
200 ppm $AgNO_3$	1.3[c]
400 ppm $AgNO_3$	0.2[c]
0 ppm $AgNO_3$, 1000 ppm ethephon + 6% urea	30.8[a]
100 ppm $AgNO_3$, 1000 ppm ethephon + 6% urea	16.8[b]
200 ppm $AgNO_3$, 1000 ppm ethephon + 6% urea	29.1[a]
400 ppm $AgNO_3$, 1000 ppm ethephon + 6% urea	20.6[ab]

[z] Means followed by the same letter are not significant, 5%.

induction in trees sprayed with 1000 ppm ethephon + 6% urea and in branch bending.

EFFECT OF ETHEPHON-UREA SPRAYS, BRANCH BENDING, AND SILVER NITRATE ON RELATIVE ETHYLENE CONTENT, LATERAL PRODUCTION, FLOWER FORMATION, FRUIT SET, AND EXTENSION GROWTH

Relative Ethylene Content

The ethylene contents of untreated guava stem tissue were relatively low (Table 3 and Figure 2). Two days after treatment, trees sprayed with 1000 ppm ethephon + 6% urea resulted in the highest ethylene content and the 100 ppm $AgNO_3$ pretreatment did not reduce this. The 200 ppm ethephon + 1% urea spray resulted in relatively lower ethylene content and was significantly different from the other treatments. Branch bending resulted in a small, but significant increase in ethylene content and 100 ppm $AgNO_3$ pretreatment reduced this (Table 3 and Figure 3).

On the 4th day, ethylene contents remained relatively high in trees sprayed with the high concentration ethephon-urea with or without $AgNO_3$ pretreatment and were significantly different from the rest of the treatments. These relatively high levels of ethylene in stem tissue were visually associated with leaf, flower, and fruit abscission which started on the second day and peaked about the 4th day. By the 7th day, very few leaves were observed on the ground. The ethylene content of stem tissue sprayed with the low concentration ethephon-urea remained at relatively low levels after four days and was significantly different from the rest of the treatments. The low levels of ethylene in these trees did not result in excessive leaf, flower, or fruit

abscission, but uniform ripening of existing mature fruits in some of the trees were observed within two weeks. After four days, ethylene content of trees stressed by branch bending returned to control levels (Table 3 and Figure 4).

After eight days, there were no significant differences in ethylene contents among trees sprayed with the low concentration ethephon-urea spray and the high concentration ethephon-urea sprays with or without $AgNO_3$ pretreatment. The increased ethylene content of trees sprayed with the low concentration ethephon-urea was the result of a second spraying five days after the first (Table 3 and Figure 5).

Trees sprayed with a 3rd, 200 ppm ethephon + 1% urea treatment one day prior to the 16th day sampling resulted in a significantly higher ethylene content compared with the other treatments. Trees sprayed with one application of 1000 ppm ethephon + 6% urea with or without $AgNO_3$ pretreatment still had low ethylene contents which were significantly different from the other treatments (Table 3 and Figure 6). After four, low concentration ethephon-urea sprays trees showed characteristic flagging of the leaves and although excessive leaf abscission did not occur at once, in some of the trees, a gradual loss of leaves resulted.

Lateral Production

Branch bending resulted in the early production of laterals and was not reduced by $AgNO_3$. Ethephon at 200 ppm + 1% urea delayed lateral emergence by about 14 days compared to branch bending and by about four days compared to the high concentration ethephon-urea spray with or without $AgNO_3$ pretreatment (Table 4).

Table 3. Effect of ethephon-urea sprays, branch bending, and silver nitrate ($AgNO_3$) on ethylene content of 'Beaumont' guava stem tissue at various sampling dates. Silver nitrate pretreatment was applied about 24 hours before the ethephon-urea spray and branch bending. Ethephon at 1000 ppm + 6% urea was applied once and ethephon at 200 ppm + 1% urea was applied four times at five day intervals.

Treatment	Ethylene (nl/g/hr)				
	Days After Treatment				
	0[z]	2	4	8	16
Control	0.7[a]	1.2[d]	1.7[c]	2.2[b]	0.2[c]
1000 ppm ethephon + 6% urea	0.0[a]	245.3[a]	162.4[a]	57.0[a]	4.0[b]
100 ppm $AgNO_3$, 1000 ppm ethephon + 6% urea	0.2[a]	294.4[a]	182.8[a]	49.8[a]	3.9[b]
200 ppm ethephon + 1% urea	0.6[a]	47.0[b]	40.8[b]	59.8[a]	29.4[a]
Branch bending	0.6[a]	7.2[c]	2.6[c]	3.6[b]	1.0[c]
100 ppm $AgNO_3$, branch bending	0.0[a]	2.5[d]	4.9[c]	2.5[b]	0.0[c]

[z] Means within columns followed by the same letter are not significant, 5%.

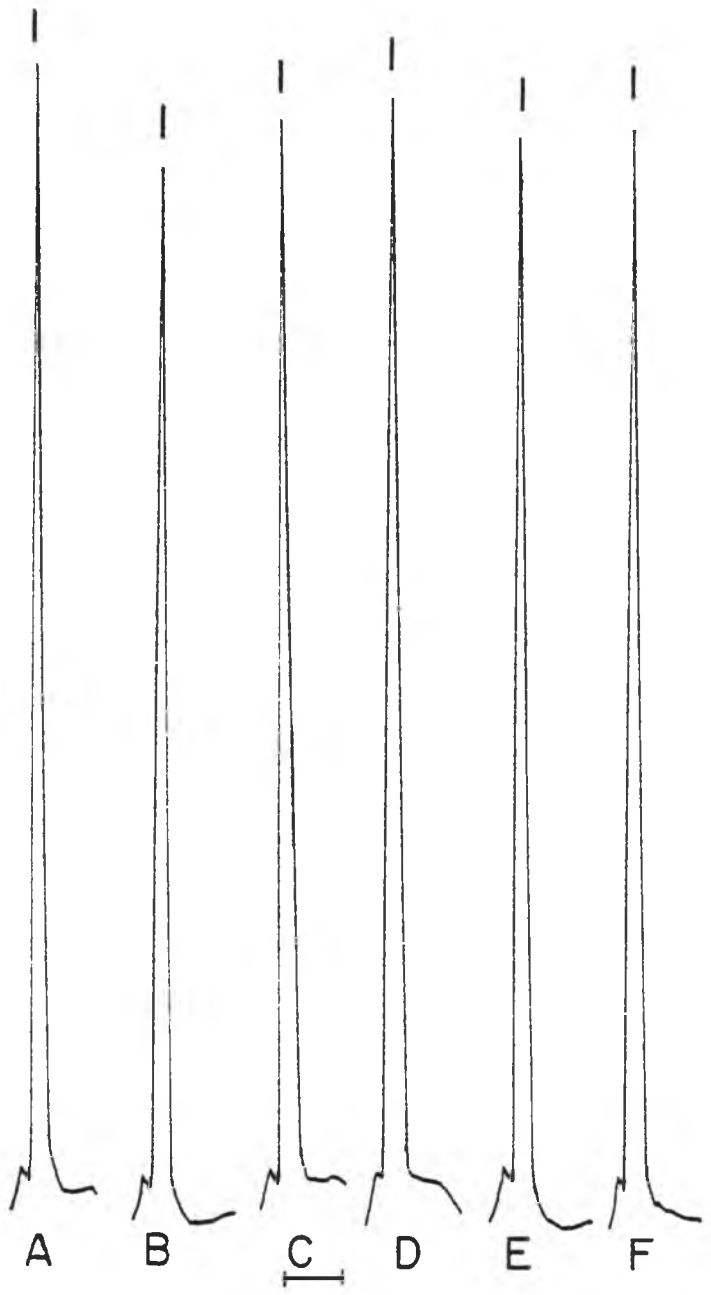

Figure 2. Selected gas chromatograms of gas samples from guava stem tissue taken prior to treatment (day 0). Peaks: 1 = unidentified. Treatments: A = control; B = 1000 ppm ethephon + 6% urea; C = 1000 ppm ethephon + 6% urea with 100 ppm $AgNO_3$ pretreatment; D = 200 ppm ethephon + 1% urea applied four times at five day intervals; E = branch bending; F = branch bending with 100 ppm $AgNO_3$ pretreatment. Chromatograms were reduced, bar represents one minute. Attenuation = X1.

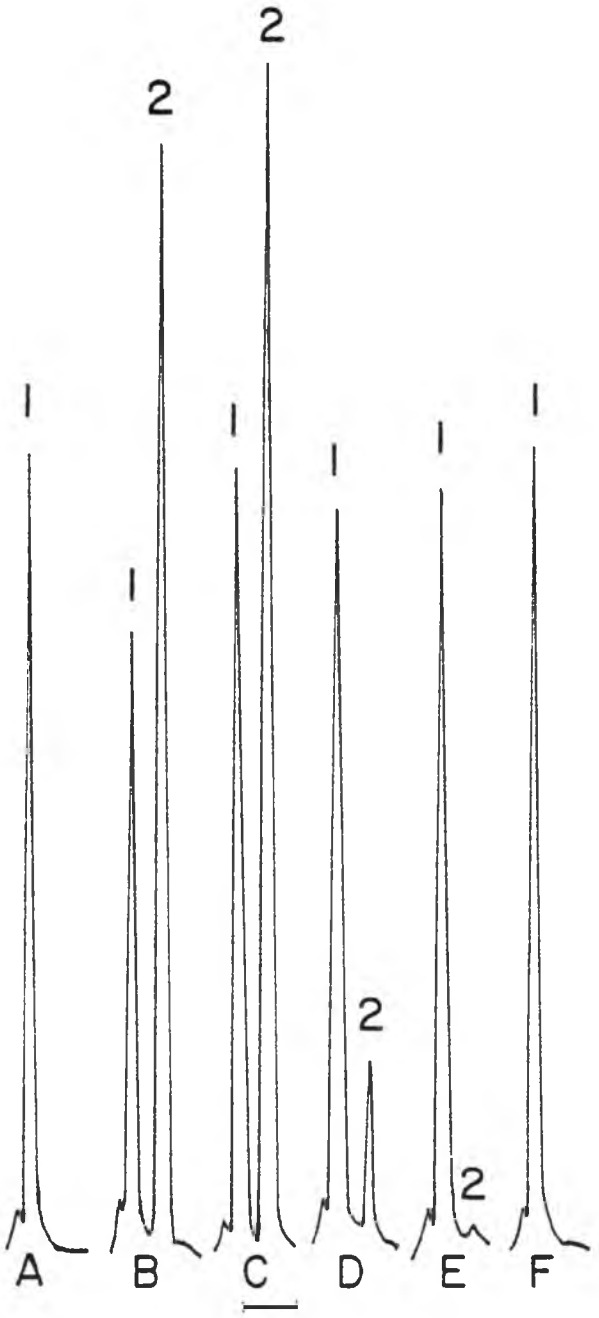

Figure 3. Selected gas chromatograms two days after treatment. Peaks: 1 = unidentified; 2 = ethylene. Selected peaks are the closest representatives of treatment means. Treatments are the same as in Figure 2. Chromatograms were reduced, bar represents one minute. Attenuation = 1X.

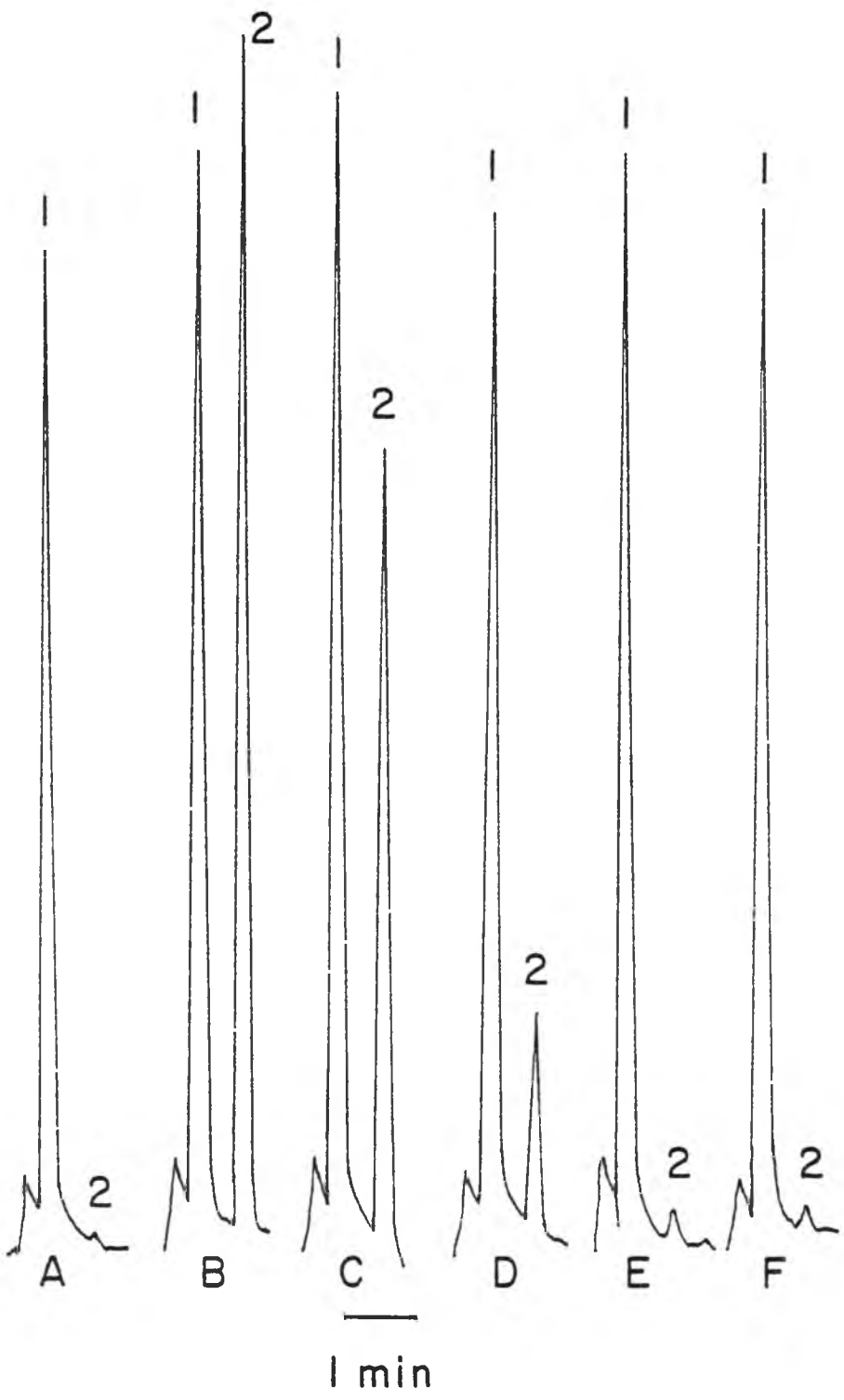

Figure 4. Selected gas chromatograms four days after treatment. Peaks: 1 = unidentified; 2 = ethylene. Selected peaks are the closest representatives of treatment means. Treatments are the same as in Figure 2. Actual size of chromatograms. Attenuation = 1X.

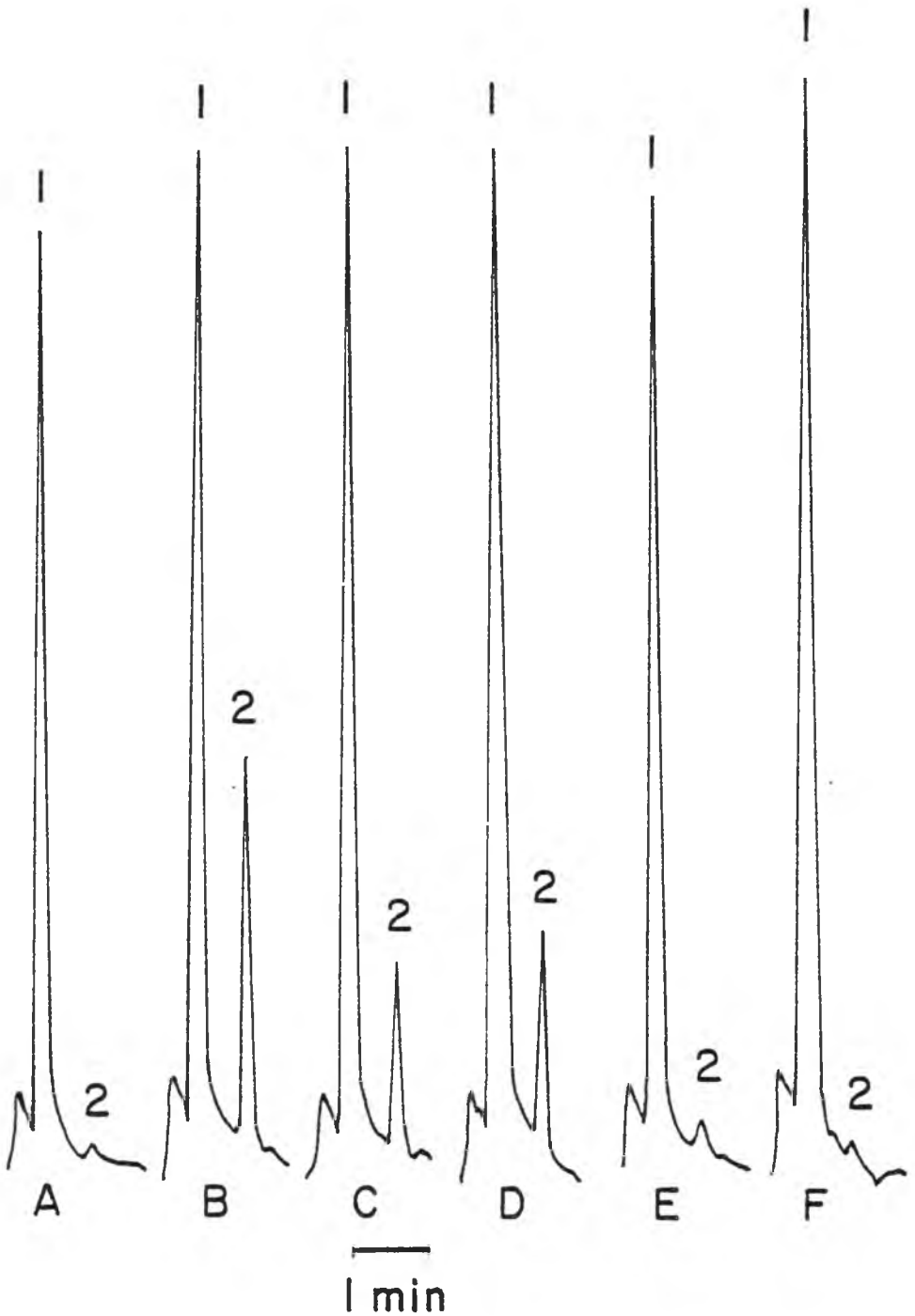

Figure 5. Selected gas chromatograms eight days after treatment. Peaks: 1 = unidentified; 2 = ethylene. Selected peaks are the closest representatives of treatment means. Treatments are the same as in Figure 2. Actual size of chromatograms. Attenuation = X1.

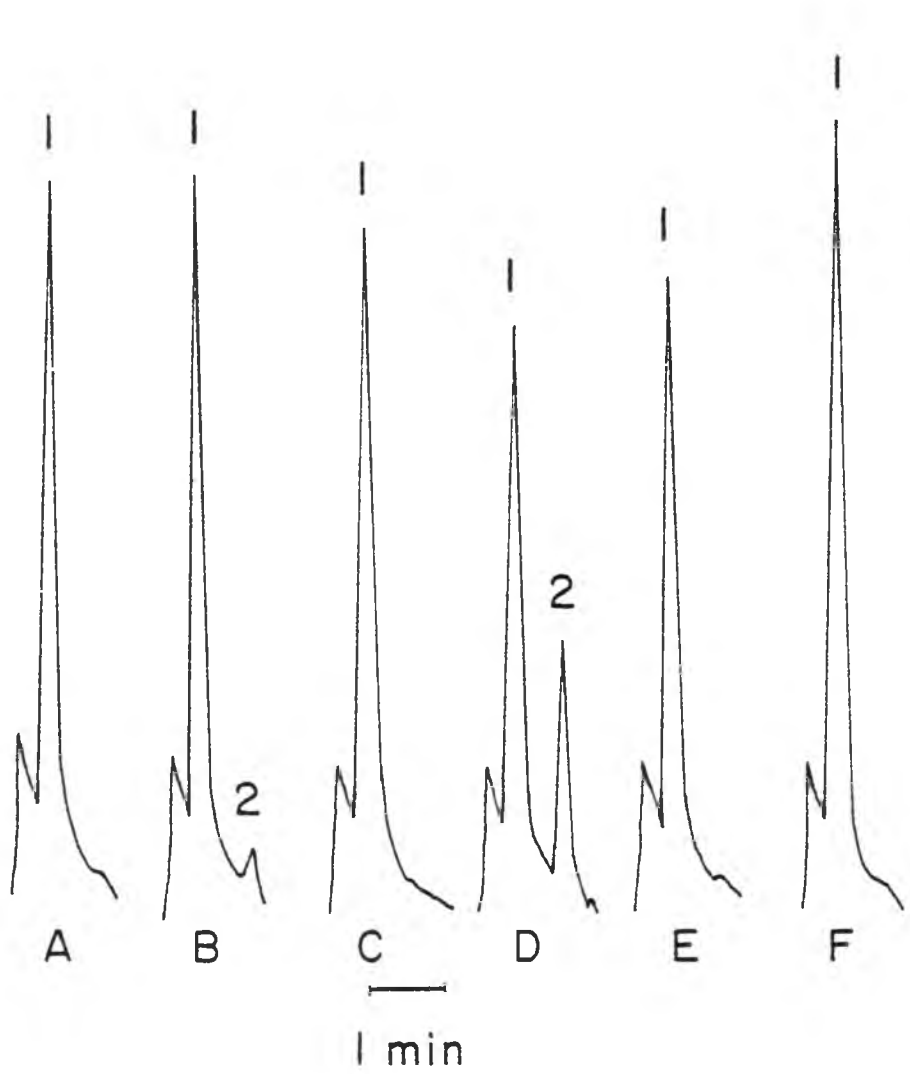

Figure 6. Selected gas chromatograms 16 days after treatment. Peaks: 1 = unidentified; 2 = ethylene. Selected peaks are the closest representatives of treatment means. Treatments are the same as in Figure 2. Actual size of chromatograms. Attenuation = 1X.

Trees sprayed with 200 ppm ethephon + 1% urea or 1000 ppm ethephon + 6% urea with $AgNO_3$ pretreatment resulted in significantly greater percentages of axillary buds producing laterals and numbers of laterals per 20 axillary buds (Table 4).

Flower Formation

Days to 50% anthesis were significantly reduced by branch bending with and without $AgNO_3$ pretreatment and significantly increased by the low concentration ethephon-urea sprays.

Branch bending with $AgNO_3$ pretreatment resulted in a significantly greater percentage of laterals which had flowers. Branch bending with or without $AgNO_3$ pretreatment, 200 ppm ethephon + 1% urea, and 1000 ppm ethephon + 6% urea with $AgNO_3$ pretreatment resulted in significantly higher numbers of flowers per 20 axillary buds. Silver nitrate increased the number of flowers over 1000 ppm ethephon + 6% urea without $AgNO_3$ pretreatment, but did not increase the number of flowers when applied prior to branch bending. Branch bending with or without $AgNO_3$ pretreatment resulted in significantly lower percentages of shoot tips with flowers (Table 5).

Fruit Set

In general, fruit set was low in all trees, but percentage fruit set in laterals of control trees was significantly higher. The number of fruits per 20 axillary buds was not significantly different between control trees and trees treated with the low concentration ethephon-urea sprays (Table 6). In all treatments, the initial fruit set appeared

Table 4. Effect of ethephon-urea sprays, branch bending, and silver nitrate ($AgNO_3$) on lateral production in 'Beaumont' guava. Silver nitrate pretreatment was applied about 24 hours before the ethephon-urea spray and branch bending. Ethephon at 1000 ppm + 6% urea was applied once and ethephon at 200 ppm + 1% urea was applied four times at five day intervals.

Treatment	Parameter		
	Days to lateral emergence[z]	% of axillary buds forming laterals	No. of laterals per 20 axillary buds
Control	20.1[b]	4.6[b]	1.0[b]
1000 ppm ethephon + 6% urea	21.1[b]	8.6[ab]	1.7[ab]
100 ppm $AgNO_3$, 1000 ppm ethephon + 6% urea	19.1[b]	12.0[a]	2.4[a]
200 ppm ethephon + 1% urea	25.5[a]	12.0[a]	2.4[a]
Branch bending	11.1[c]	6.0[ab]	1.2[b]
100 ppm $AgNO_3$, branch bending	11.7[c]	6.6[ab]	1.3[b]

[z] Means within columns followed by the same letter are not significant, 5%.

Table 5. Effect of ethephon-urea sprays, branch bending, and silver nitrate ($AgNO_3$) on flower formation in 'Beaumont' guava. Silver nitrate pretreatment was applied about 24 hours before the ethephon-urea spray and branch bending. Ethephon at 1000 ppm + 6% urea was applied once and ethephon at 200 ppm + 1% urea was applied four times at five day intervals.

Treatment	Parameter			
	Days to 50% anthesis[z]	% of laterals with flowers	No. of flowers per 20 axillary buds	% of shoot tips with flowers
Control	78.6[b]	82.5[bc]	2.4[c]	44.3[a]
1000 ppm ethephon + 6% urea	76.8[b]	71.0[cd]	2.8[bc]	37.1[a]
100 ppm $AgNO_3$, 1000 ppm ethephon + 6% urea	74.6[b]	79.5[cd]	5.5[a]	52.6[a]
200 ppm ethephon + 1% urea	84.2[a]	67.6[d]	4.1[ab]	45.1[a]
Branch bending	64.6[c]	92.1[ab]	4.1[ab]	20.5[b]
100 ppm $AgNO_3$, branch bending	62.6[c]	96.1[a]	4.7[a]	18.0[b]

[z] Means within columns followed by the same letter are not significant, 5%.

Table 6. Effect of ethephon-urea sprays, branch bending, and silver nitrate ($AgNO_3$) on fruit set in 'Beaumont' guava. Silver nitrate pretreatment was applied about 24 hours before the ethephon-urea spray and branch bending. Ethephon at 1000 ppm + 6% urea was applied once and ethephon at 200 ppm + 1% urea was applied four times at five day intervals.

Treatment	Parameter		
	% fruit set in laterals[z]	No. of fruits per 20 axillary buds in laterals	% fruit set in shoot tips
Control	30.0[a]	0.7[a]	12.6[a]
1000 ppm ethephon + 6% urea	4.6[bc]	0.2[bc]	5.9[a]
100 ppm $AgNO_3$, 1000 ppm ethephon + 6% urea	6.0[bc]	0.3[bc]	13.8[a]
200 ppm ethephon + 1% urea	12.4[b]	0.4[ab]	12.7[a]
Branch bending	4.4[bc]	0.1[bc]	—
100 ppm $AgNO_3$, branch bending	2.4[c]	0.1[c]	—

[z] Means within columns followed by the same letter are not significant, 5%.

high, but many of the fruits dropped about one month after anthesis when they were about 1.5 cm in length.

Extension Growth

There were significant differences in extension growth 18 days after treatment. Ethephon at 1000 ppm + 6% urea with or without $AgNO_3$ pretreatment and ethephon at 200 ppm + 1% urea reduced extension growth compared to controls. Branch bending with or without $AgNO_3$ did not reduce growth 18 days after treatment. After 79 and 140 days, no significant differences in extension growth were measured (Table 7).

Simple Linear Correlations

There was a highly significant correlation between ethylene content in guava stem tissue samples taken two days after treatment and the number of laterals per 20 axillary buds. There was also a highly significant correlation between the number of laterals per 20 axillary buds and the number of flowers per 20 axillary buds, but the correlation between ethylene content two days after treatment and the number of flowers per 20 axillary buds was not significant.

There was a highly significant negative correlation between ethylene content two days after treatment and extension growth 18 days after treatment, but extension growth 18 days after treatment was not negatively correlated with number of flowers per 20 axillary buds.

The number of flowers per 20 axillary buds was not negatively correlated with percentage fruit set in laterals (Table 8).

Table 7. Effect of ethephon-urea sprays, branch bending, and silver nitrate ($AgNO_3$) on extension growth in 'Beaumont' guava. Silver nitrate pretreatment was applied about 24 hours before the ethephon-urea spray and branch bending. Ethephon at 1000 ppm + 6% urea was applied once and ethephon at 200 ppm + 1% urea was applied four times at five day intervals.

Treatment	Extension Growth (cm)		
	Days After Treatment		
	18[z]	79	140
Control	6.1[a]	28.9[a]	31.5[a]
1000 ppm ethephon + 6% urea	2.0[bc]	23.1[a]	33.1[a]
100 ppm $AgNO_3$, 1000 ppm ethephon + 6% urea	1.4[c]	22.6[a]	30.0[a]
200 ppm ethephon + 1% urea	1.9[bc]	20.2[a]	25.6[a]
Branch bending	4.6[ab]	23.1[a]	30.5[a]
100 ppm $AgNO_3$, branch bending	3.5[ab]	22.9[a]	29.0[a]

[z] Means within columns followed by the same letter are not significant, 5%.

Table 8. Simple linear correlations.

Parameters	r^z	n
1. Ethylene content two days after treatment with no. of flowers per 20 axillary buds.	0.09^{ns}	48
2. Extension growth 18 days after treatment with no. of flowers per 20 axillary buds.	-0.12^{ns}	48
3. Ethylene content two days after treatment with extension growth 18 days after treatment.	-0.48**	48
4. No. of laterals per 20 axillary buds with no. of flowers per 20 axillary buds.	0.59**	48
5. Ethylene content two days after treatment with no. of laterals per 20 axillary buds.	0.52**	48
6. No. of flowers per 20 axillary buds with percentage fruit set in laterals.	-0.28^{ns}	48

[z] ** Highly significant, 1%. [ns] Not significant.

DISCUSSION

Ethylene induced responses are known to have threshold, half-maximal, and near maximal responses at low levels of the gas and the responses are intensified as the levels are increased (38). Higher ethylene contents in guava stem tissue were not associated with an increase in flower formation. Branch bending with $AgNO_3$ pretreatment resulted in significantly lower ethylene content, but greater number of flowers than the high concentration ethephon-urea spray without $AgNO_3$. Silver nitrate inhibited production of ethylene in bent guava branches two days after treatment, but flowering was not reduced. These results suggest that ethylene is not directly associated with an increase in flowering in guava.

The time course of leaf abscission for ethylene gas and for ethephon are similar (104). The high concentration ethephon-urea spray without $AgNO_3$ pretreatment resulted in excessive leaf abscission, but branch bending with $AgNO_3$ pretreatment did not result in excessive leaf abscission and flowering was greater. This suggests that leaf abscission is not directly associated with flower induction in guava. Silver nitrate reduces leaf abscission caused by the high concentration ethephon-urea spray and therefore photosynthesis can still occur. The presence of adequate carbohydrate reserves during flower initiation is essential for the process to occur (81, 164). This may be a critical factor in young guava trees which have already produced flowers and fruits. High concentration ethephon-urea sprays in this situation may stimulate vegetative rather than flowering laterals. In other fruit

trees, it is also suggested that the leaves are necessary for the production of the flowering stimulus (50, 126, 127, 144) or may be necessary to maintain an active transport system to the axillary buds (97).

A reduction in shoot growth was not associated with an increase in flowering. Branch bending with $AgNO_3$ did not result in a reduction in extension growth 18 days after treatment, but resulted in relatively higher flower formation. Ethephon-urea sprays resulted in a reduction in shoot growth 18 days after treatment, but the high concentration ethephon-urea spray without $AgNO_3$ did not result in an increase in flower formation which suggests that a reduction in shoot growth is not directly associated with an increase in flowering.

In this experiment, the more laterals produced, the greater the number of flowers. Flower induction in some fruit trees is associated with a temporary reduction in apical dominance which results in the mobilization of metabolites to the lateral buds rather than to the shoot tip. Ethephon is known to reduce apical dominance by producing ethylene which inhibits auxin metabolism and transport. Ethylene also inhibits lateral bud growth when it is present, but stimulates the production of laterals when the treatments are terminated (45, 164). Similar effects are observed in guava.

The effect of four, low concentration ethephon-urea sprays on lateral bud development was evident by the time it took for the laterals to grow out. This treatment and 1000 ppm ethephon + 6% urea with $AgNO_3$ pretreatment both resulted in significantly greater numbers of laterals and of flowers produced. In guava, the higher the ethylene

content, the greater the reduction in apical dominance and the greater the number of laterals produced.

Bending resulted in the early stimulation of lateral bud growth on the upper side of branches. The inhibition of bud growth on the underside of branches may have been due to the lateral movement of auxin from the upper to the lower side by gravity (106, 107) and which may have stimulated the production of ethylene. It is known that ethylene production occurs in areas with high auxin and ethylene contents in horizontal branches are higher in the shoot tips and on the underside of branches (5, 128, 157). In vertical branches, auxin moves in a polar manner and inhibits lateral bud growth (122).

Laterals on bent guava branches were usually produced from leafless axillary buds. In most plants, the older leaves proximal on the branch naturally abscise first which may be due to a decline in the amount of auxin transported into the petiole and to an increasing sensitivity to ethylene (26, 74). It is also known that the concentration of auxin decreases with increasing distance from the shoot tip (107). This may be why the laterals in bent guava branches were produced from the axillary buds of leafless, older wood rather than from the axillary buds subtended by leaves closer to the stem apex. Branch bending in guava may have reduced the amount of auxin present at the upper side of the branches so that the buds could become sinks for metabolites necessary to start growth and flower initiation, therefore, most of the laterals which grew out had flowers buds in the leaf axils. In some branches, very few laterals were produced and this may have been due to the presence of fruits prior to and during bending. If the branches were

not very vigorous branch bending would also have had no effect on the production of laterals and flowers (148, 164).

Increased flower production was not associated with decreased fruit set. A decrease in fruit set in treated trees may have been the result of competition for nutrients between fruits and new vegetative growth. Fruit drop was also observed after insecticides were applied which may have damaged the developing fruits. Although the reason for the fruit drop is not known, it is not a phenomena specific to guava and occurs in other fruit crops, for example, in apples the period of high fruit abscission is known as the June drop (97).

It seems that in guava, as in other fruit trees, a reduction in apical dominance, which is usually associated with a reduction in terminal growth, allows the development of axillary buds so that flower initiation can take place provided that sufficient quantities of carbohydrates are present. A reduction in apical dominance can be brought about by environmental stresses and by cultural practices such as ethephon-urea sprays, pruning, branch bending, and withholding water followed by fertilization and irrigation. The environmental conditions, tree vigor, and availability of resources would determine which cultural practice to use for an integrated system. It should be stressed that asexually propagated trees would be more responsive to environmental factors and to cultural practices which induce flower formation. Although seedling trees are easier and cheaper to grow, their genetic variability and their stage of juvenility would limit their response to flower formation stimuli which would initiate flowering in mature, asexually propagated trees.

SUMMARY

1. Leaf abscission was reduced by 200 ppm ethephon + 1% urea compared with 1000 ppm ethephon + 6% urea.
2. Silver nitrate at 100 ppm reduced leaf abscission induced by 1000 ppm ethephon + 6% urea.
3. Ethephon at 1000 ppm + 6% urea with and without 100 ppm silver nitrate pretreatment resulted in significantly higher ethylene contents in stem tissue. Silver nitrate pretreatment increased lateral production and flower formation over controls.
4. Ethephon at 200 ppm + 1% urea applied four times at five day intervals resulted in an increase in lateral production and flower formation over controls. Number of fruits was not significantly different from controls.
5. Two days after treatment, branch bending resulted in an increase in stress ethylene production and was reduced by 100 ppm silver nitrate pretreatment. Branch bending with and without silver nitrate pretreatment resulted in an increase in flowering over controls.
6. Ethylene content in stem tissue was positively correlated with number of laterals produced and negatively correlated with extension growth.
7. Ethylene content was not correlated with flowering.
8. Reduction in growth was not correlated with flowering.
9. Number of laterals was positively correlated with number of flowers which suggests that a reduction in apical dominance is associated with flower induction in young, clonal guava trees.

APPENDIX

Appendix Table 9. Analysis of variance table for the effect of ethephon-urea sprays on leaf abscission in 'Beaumont' guava trees seven days after treatment.

Source of variation	DF	F^z
Treatments	4	14.10^{*}
Replications	1	0.11^{ns}
Error	4	2.48^{ns}
Sampling error	40	
C. V. (%)		76.15
$S_{\bar{y}}$		5.83

^{z} * Significant, 5%. ^{ns} Not significant.

Appendix Table 10. Analysis of variance table for the effect of silver nitrate on ethephon-urea induced leaf abscission in 'Ka hua kula' guava trees seven days after treatment.

Source of variation	DF	F^z
Treatments	7	45.66^{**}
Replications	1	1.70^{ns}
Error	7	1.33^{ns}
Sampling error	64	
C. V. (%)		41.50
$S_{\bar{y}}$		2.10

[z] ** Highly significant, 1%. [ns] Not significant.

Appendix Table 11. Analysis of variance tables for the effect of ethephon-urea sprays, branch bending, and silver nitrate on ethylene content of 'Beaumont' guava stem tissue at various sampling dates.

	Days After Treatment									
	0		2		4		8		16	
Source of variation	DF	F[z]	DF	F	DF	F	DF	F	DF	F
Treatments	5	0.82[ns]	5	89.42**	5	58.55**	5	51.37**	5	55.00**
Replications	7	1.19[ns]	7	1.63[ns]	7	0.82[ns]	7	0.73[ns]	7	1.74[ns]
Error	35		35		33		35		35	
C. V. (%)	—		22.56		27.41		24.70		41.82	
$S_{\bar{y}}$	—		0.10		0.12		0.096		0.072	

[z] ns Not significant. ** Highly significant, 1%.

Appendix Table 12. Analysis of variance tables for the effect of ethephon-urea sprays, branch bending, and silver nitrate on lateral production in 'Beaumont' guava.

	Parameter					
	Days to lateral emergence		% of axillary buds forming laterals		No. of laterals per 20 axillary buds	
Source of variation	DF	F[z]	DF	F	DF	F
Treatments	5	33.0**	5	7.47**	5	6.5**
Replications	7	0.3[ns]	7	0.85[ns]	7	0.9[ns]
Error	35	2.0**	35	2.68**	35	2.8**
Sampling error	125		143		141	
C. V. (%)	29.56		43.77		20.3	
$S_{\bar{y}}$	1.25		1.52		0.24	

[z] ** Highly significant, 1%. [ns] Not significant.

Appendix Table 13. Analysis of variance tables for the effect of ethephon-urea sprays, branch bending, and silver nitrate on flower formation in 'Beaumont' guava.

	Parameter							
	Days to 50% anthesis[z]		% of laterals with flowers		No. of flowers per 20 axillary buds		% of shoot tips with flowers	
Source of variation	DF	F[z]	DF	F	DF	F	DF	F
Treatments	5	24.0**	5	6.08**	5	4.8**	5	8.79**
Replications	7	0.5[ns]	7	1.12[ns]	7	1.3[ns]	7	3.13*
Error	35	4.0**	35	3.35**	35	2.3**	35	1.61*
Sampling error	134		141		141		143	
C. V. (%)	12.79		35.22		74.62		67.73	
$S_{\bar{y}}$	1.70		4.38		0.52		4.08	

[z] ** Highly significant, 1%. * Significant, 5%. [ns] Not significant.

Appendix Table 14. Analysis of variance tables for the effect of ethephon-urea sprays, branch bending, and silver nitrate on fruit set in 'Beaumont' guava.

	Parameter					
	% fruit set in laterals[z]		No. of fruits per 20 axillary buds in laterals		% fruit set in shoot tips	
Source of variation	DF	F[z]	DF	F	DF	F
Treatments	5	8.95**	5	5.35**	5	1.87[ns]
Replications	7	1.27[ns]	7	1.00[ns]	7	0.65[ns]
Error	35	2.34**	35	1.13[ns]	21	0.65[ns]
Sampling error	141		141		85	
C. V. (%)	126.73		169.97		—	
$S_{\bar{y}}$	3.07		0.091		—	

[z] ** Highly significant, 1%. [ns] Not significant.

Appendix Table 15. Analysis of variance tables for the effect of ethephon-urea sprays, branch bending, and silver nitrate on extension growth in 'Beaumont' guava.

	Days After Treatment					
	18		79		140	
Source of variation	DF	F[z]	DF	F	DF	F
Treatments	5	3.87**	5	0.72[ns]	5	0. 84[ns]
Replications	7	1.28[ns]	7	0.76[ns]	7	0.61[ns]
Error	35		35		35	
C. V. (%)	51.67		—		—	
$S_{\bar{y}}$	0.097		—		—	

[z] ** Highly significant, 1%. [ns] Not significant.

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